WING HOMOEOSIS IN *PARARGE AEGERIA* L. (LEPIDOPTERA: SATYRIDAE)

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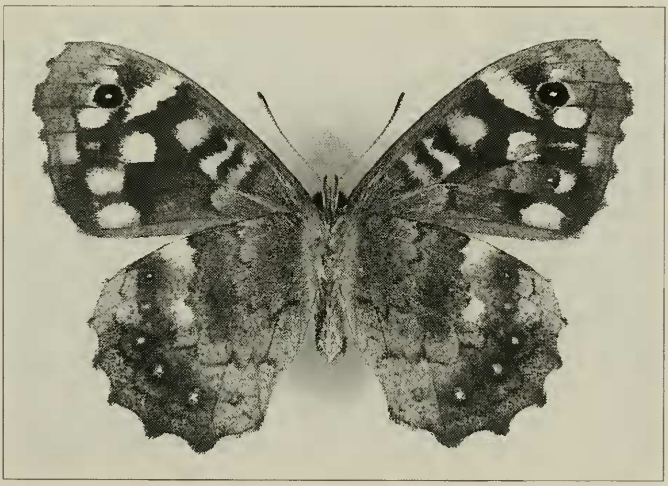
A female speckled wood butterfly, *Pararge aegeria* L. subspecies *oblita* Harrison, emerged 2.x.1995 among a bred stock derived from two females collected at Glen Lonan, east of Oban, Argyll, 18–25.viii.1993 (56° 24′ N, 5° 22′ W). Pattern typical of left hindwing underside spaces 2 and 3 (s2 and s3) was reproduced at corresponding positions in left forewing underside s2 and s3 (Fig. 1). There was no corresponding pattern transformation on the right forewing underside nor on the upper surface.

Homoeosis refers to the development of tissue typical of one part of an organism at a position typical of another tissue type. In Lepidoptera this is typically recognized by an area on one wing showing the pattern of another wing. Homoeosis is rare in Lepidoptera (Ford, 1957) but has been reported in several families including the Satyridae.

Insect forewings belong to the middle thoracic segment or mesothorax, and the hindwings to the hind thoracic segment or metathorax. The incidence of different types of homoeotic transformation in Lepidoptera, has revealed also that each wing is divided further into anterior and posterior developmental units or 'compartments', along a baso-distal axis that borders s5 and s6 (Sibatani, 1980). In the following discussion, s1 to s5 on the forewing and s1 to s4 on the hindwing represent the 'posterior' of the respective wing, while the forewing area between s6 and the costa and the hindwing area between s5 and the costa represent the 'anterior' of the respective wing.

The most common type of homoeosis in Satyridae concerns the presence within the underside posterior hindwing of the underside posterior forewing pattern. The present case is unusual therefore in demonstrating the presence within the underside posterior forewing of underside posterior hindwing pattern, analogous to



contra-bithorax transformations in the fruit fly, *Drosophila melanogaster* L. (in which the posterior section of the middle thoracic segment shows features of the posterior section of the hind thoracic segment) (Sibatani, 1980).

Insect homoeoses and segmentation abnormalities are informative because they provide insights into the development and evolution of biological patterns (Sibatani, 1980; Ho, 1989). In Lepidoptera, each wing develops from a group of primordial cells known as an imaginal disc (Ford, 1957). The presence of homoeosis on one surface only is typical of homoeotic transformations in Lepidoptera, and points to the establishment, very early in development, of independence between upperside and underside compartments within each wing disc. As homoeosis can involve an area of forewing pattern appearing on the hindwing, independence between forewing and hindwing discs must therefore be established later, and consequently homoeotic transformations on one surface between fore- and hind-wing are commoner than transformations between the two surfaces.

In the present case, the transformation involved corresponding compartments (namely posterior compartments, these include s2 and s3) within each respective wing disc. This suggests that prior to the establishment of independence between fore- and hind-wing, the anterior compartments of both wings function collectively as one developmental unit and the posterior compartments as another (cf. Ho, 1989).

Hence symmetry with left/right independence is the first distinction to be established, and in multicellular animals occurs in early egg development (Goodwin, 1984; Sibatani, 1980). This is followed by upperside/underside independence, then corresponding (and likely coordinated) anterio-posterior distinctions within each disc (cf. Ho, 1989). Lastly forewing/hindwing independence is established (Sibatani, 1980).

The cause of homoeotic transformation in the present *P. aegeria oblita* has yet to be firmly established. Ford (1957) suggested that homoeosis in Lepidoptera might result from genetic mutation. However, a mutant gene could be expected to affect both sides similarly because each gene is copied during embryonic cell division into every cell of a given individual, and no deviations from left/right symmetry (other than minor, random discrepancies resulting from developmental disturbances) are known in Lepidoptera (Winokur & White, in prep.). In *Drosophila*, chemical agents can produce effects that mimic, i.e. 'phenocopy', the effects of genetic homoeotic mutants. However, contra-bithorax phenocopies are produced more readily in *Drosophila* by the short-term application of high temperatures or 'heat shock' than by exposing immature stages to organic compounds such as ether (Sibatani, 1980). The comparable transformation in *P. aegeria oblita* therefore, might similarly represent an effect of unusually high temperature.

The stock was reared outdoors on cultivated wood false brome grass, *Brachypodium sylvaticum* L., at Worksop, Nottinghamshire (53° 19′ N, 1° 7′ W) until 25.viii.1995 when the stock was divided and the rearing of a sample was continued similarly at Reading, Berkshire (51° 27′ N, 0° 56′ W). Though temperatures were not recorded, ongoing temperatures in S. England during July and August 1995, when the affected individual would have been a larva or young pupa, were reported by the Meteorological Office (via the media) to have been the hottest for many years. Moreover, since annual July and August temperatures are generally higher in S. England than in N.W. Scotland where the stock originated, *P. aegeria oblita* is expected to be less well suited to developing under such temperatures than S. England *P. a. tircis* Butler (Winokur, 1995).

A further factor affecting developmental stability in the species is inbreeding (Oliver, 1981). The stock was originated in August 1993, the F_1 emerged in July 1994 and the F_2 in September, and the F_3 started to emerge in July 1995; the present individual (emerging October 1995) thus represents an F_4. Oliver (1981) found that inbreeding depression in *P. aegeria* (as evidenced by the percentage of fertilized eggs failing to hatch) increased with inbreeding, and suggested that inbreeding in the species may reduce the genetic balance of individuals and consequently developmental stability. However, further investigation will be required before firm conclusions can be drawn, and the stock is being continued in the hope that it might yield further insights into the nature of wing homoeosis in *Pararge aegeria*.

Acknowledgement

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BOOK REVIEWS

Collins field guide. Spiders of Britain and northern Europe by Michael J. Roberts. London, HarperCollins, 1995, 384 pp, 32 colour plates, hardback, £14.99.—The book reckons to cover over 450 species, all but the very difficult black 'money' spiders, a few far northern endemics and southern rarities. Of these 247 are illustrated in colour. A tightly packed introduction on spiders and how to study them is followed by the main text. Within this are keys to families and genera. Each species has brief description and notes on habitat and distribution and every entry has a very detailed drawing of male palp and female epigyne. As a popular field guide, this book is probably one of the most important to be published in recent years since it suddenly brings serious arachnology within reach of so many people. Roberts' previous book, *The spiders of Great Britain and Ireland* published by Harley Books in 1985–7, became the great authoritative work on these creatures, but its price and complexity put it beyond the reach of many, especially the more casual observers who ought to buy the Collins guide. My only gripe is with the colour figures, where every plate has spiders painted similar sizes, even though they may be of completely different sizes in life. Thus, for example, we have *Scytodes thoracica* (3–5 mm) shown larger than and right next door to *Pholcus phalangioides* (8–10 mm). Although the plate captions give dimensions in millimetres, this is nothing compared to the visual reference of a life-size silhouette or size-range bars.

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